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CONTROLS OVER FOLIAR N:P RATIOS IN TROPICAL RAIN FORESTS

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Abstract. Correlations between foliar nutrient concentrations and soil nutrient availability have been found in multiple ecosystems. These relationships have led to the use of foliar nutrients as an index of nutrient status and to the prediction of broadscale patterns in ecosystem processes. More recently, a growing interest in ecological stoichiometry has fueled multiple analyses of foliar nitrogen : phosphorus (N:P) ratios within and across ecosystems. These studies have observed that N:P values are generally elevated in tropical forests when compared to higher latitude ecosystems, adding weight to a common belief that tropical forests are generally N rich and P poor. However, while these broad generalizations may have merit, their simplicity masks the enormous environmental heterogeneity that exists within the tropics; such variation includes large ranges in soil fertility and climate, as well as the highest plant species diversity of any biome. Here we present original data on foliar N and P concentrations from 150 mature canopy tree species in Costa Rica and Brazil, and combine those data with a comprehensive new literature synthesis to explore the major sources of variation in foliar N:P values within the tropics. We found no relationship between N:P ratios and either latitude or mean annual precipitation within the tropics alone. There is, however, evidence of seasonal controls; in our Costa Rica sites, foliar N:P values differed by 25% between wet and dry seasons. The N:P ratios do vary with soil P availability and/or soil order, but there is substantial overlap across coarse divisions in soil type, and perhaps the most striking feature of the data set is variation at the species level. Taken as a whole, our results imply that the dominant influence on foliar N:P ratios in the tropics is species variability and that, unlike marine systems and perhaps many other terrestrial biomes, the N:P stoichiometry of tropical forests is not well constrained. Thus any use of N:P ratios in the tropics to infer larger-scale ecosystem processes must comprehensively account for the diversity of any given site and recognize the broad range in nutrient requirements, even at the local scale.

Key words: Brazil; Costa Rica; foliar nitrogen; foliar phosphorus; N:P ratio; nutrient limitation; tropical rain forest.

Introduction

Theoretical connections between foliar element concentrations and soil fertility have been a cornerstone of ecosystem science for years (Vitousek 1982, 1984, Field and Mooney 1986), and multiple studies have shown that leaf nutrients, especially nitrogen (N) and phosphorus (P), reflect soil nutrient availability (e.g., Vitousek and Farrington 1997, Aerts and Chapin 2000, Hobbie and Gough 2002, Vitousek 2004). Thus foliar N and P concentrations are often viewed as an index of nutrient status that may provide insight into processes such as net primary productivity (NPP), decomposition, nutrient mineralization, trace gas emissions, and leaching losses. More recently, a growing focus on ecological stoichiometry (Sterner and Elser 2002) has led to a broader use of N:P ratios in leaves to infer potential nutrient limitation of terrestrial NPP (Koerselmann and Mueleman 1996, Tessier and Raynal 2003, Güsewell 2004, Reich and Oleskyn 2004, Richardson et al. 2004).

Three independent analyses summarized in Hedin (2004) showed an increase in foliar N:P values with decreasing latitude, adding support to a widely held belief in ecosystem ecology that tropical forests generally are N rich but P poor (Hedin 2004), and that plants in tropical habitats are more P than N limited (Reich and Oleskyn 2004). These generalizations owe much to prior analyses of leaf litter nutrients (e.g., Vitousek 1982, Vitousek and Sanford 1986), N trace gas emissions (Matson and Vitousek 1987, Keller et al. 1988), syntheses of foliar $\delta^{15}N$ (Martinelli et al. 1999), and a few direct tests of nutrient limitation in tropical forests (e.g., Herbert and Fownes 1995, Vitousek and Farrington 1997, Cleveland et al. 2002). Taken as a whole, multiple lines of evidence support the relatively N-rich, P-poor picture of tropical forests (Vitousek 1984,

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Robertson 1989, Sollins 1998, Matson et al. 1999, Paoli et al. 2005), and thus the increase in foliar N:P values in equatorial latitudes makes intuitive sense.

However, the Vitousek and Sanford (1986) paper, among others, highlights another aspect of the tropical forest biome that is too often ignored: its remarkable environmental heterogeneity. The tropical forest biome contains every major soil order (Sanchez et al. 1982), a fourfold range in mean annual precipitation (Schuur 2003), and a mean annual temperature range that exceeds 15°C. Its exceptional biodiversity is well publicized (e.g., Wilson 1988), and thus the potential for species-driven variation in nutrient cycling is notably high. Arguably, tropical forests are the most biogeochemically diverse biome on the planet, and therefore broad generalizations about the nature of nutrient limitation are perhaps most difficult and dangerous here.

These facts offer a substantial challenge to interpreting the meaning of foliar N and P values in tropical forests. Multiple published studies (e.g., Koerselmann and Mueleman 1996, Güsewell 2004, Reich and Oleskyn 2004) propose that low foliar N:P values should reflect N limitation, while high N:P values likely reflect P limitation, and suggest that the transition between these states exists at N:P ratios of ~14–16 (mass basis). Thus the higher average N:P values in equatorial latitudes have been interpreted as further evidence of widespread P limitation in tropical ecosystems (Hedin 2004, Reich and Oleskyn 2004). However, foliar N:P ratios are not simply a function of soil availability (a fact not ignored in these global analyses). Variation in climate, life history traits, and herbivory, among others, can regulate foliar chemistry (Reich et al. 1999, Martinelli et al. 2000, Wright et al. 2001, Ackerly et al. 2002, Bowman et al. 2003, Reich et al. 2003, Wright et al. 2004).

Thus unraveling the major controls over foliar N:P values may be particularly difficult in the tropics, not only due to their high species and environmental diversity, but also because of a paucity of data. For example, Reich and Oleskyn (2004) assembled a remarkable data set that includes 1280 species across 452 sites. However, only seven of those sites were in mature tropical forests, representing a total of 112 tree species, and only 11 of those species represented the entirety of continental forests in Latin America and Africa. Similarly, the McGroddy et al. (2004) comparison of mean foliar N:P values in tropical vs. temperate forests included 48 temperate sites, but only seven from the tropics. These imbalances do not reflect poorly on the authors; data from the tropics, especially lowland continental forests, are simply scarce.

Our interest was to explore the primary sources of variation in tropical forest N:P ratios, as a step toward a better understanding of where and how foliar chemistry in the tropics can be used as an index of nutrient limitation and ecosystem processes. Here we approached this task in two ways. First, we analyzed foliar N and P content from 150 canopy tree species across sites in the Brazilian Amazon and Costa Rica. These data were then combined with a new synthesis of published values from 47 tropical forest sites to address several questions: (1) Do foliar N:P values reflect broad differences in soil nutrient status? (2) How does within-site and within-family species variability in foliar N:P ratios compare to that caused by soil type and climate? (3) Do foliar N:P ratios vary with latitude and mean annual rainfall within the tropical biome? (4) Do foliar N and/or P concentrations vary with seasonal changes in rainfall?

Materials and Methods

Site descriptions

We measured foliar N and P concentrations in mature canopy trees located in five lowland tropical rain forest sites. Three of these were on the Osa Peninsula in southwest Costa Rica; the other two were located in the Brazilian Amazon. Two of the Costa Rican sites are located just east of the town of Agujitas, Drake Bay, on the north end of the Osa Peninsula (8°43′ N, 83°37′ W) in highly diverse primary forests. They are <10 km from the Pacific Ocean, have a mean annual temperature (MAT) of ~26°C that varies by <1.5°C annually, and receive a mean annual precipitation (MAP) of ~5000 mm/yr. A short but significant dry season typically occurs between December and March of each year, when monthly precipitation averages <200 mm (Cleveland et al. 2006). The two sites are within 500 m of each other but are characterized by distinct soil orders and categories of parent material (Bern et al. 2005). One site (UF) possesses Ultisols (Perez et al. 1978) that developed on a steeply dissected landscape in the Osa basaltic complex; the other site (MF) contains a less weathered alluvial Mollisol that developed from a complex mixture of Quaternary alluvium dominated by Osa basalt (Berrange and Thorpe 1988, Bern et al. 2005). A third site (AB) is also located on Ultisols of similar origin to the UF site, and is located ~5 km from the town of Rincón near the Golfo Dulce, and ~30 km from the UF and MF sites (Bern et al. 2005). Additional details on site and soil characteristics can be found in Cleveland et al. (2002) and Bern et al. (2005).

Foliar N and P were also assayed in leaves taken from two mature forest stands in the Brazilian Amazon. One site was located on the Fazenda Cauaxí in the Paragominas Municipality of Pará State, Brazil, in the eastern Amazon (3°44′ S, 48°17′ W). The climate of the Cauaxí region is humid tropical with MAP of 2200 mm (Costa and Foley 1998). A dry season extends from July through November (generally <50 mm/month). Soils in the area are classified mainly as dystrophic yellow latosols according to the Brazilian system (RADAMBRASIL 1983); these are Oxisols in the U.S. system. The topography is flat to mildly undulating, and the forest is classified as tropical dense moist forest (IBGE 1988).

The second Brazil site was located in the Tapajós National Forest in central Pará, ~80 km south of the

city of Santarém (2°50′ S, 55°00′ W). Soils in the area range from 70% clay-dominated Oxisols and Ultisols to 30% sand-dominated Ultisols (Silver et al. 2000). MAP is ~2000 mm/yr, with most inputs occurring during the wet season from January to June (Nepstad et al. 2004).

Foliar analyses

Foliar samples were collected from full-sun portions of mature canopy trees. The Costa Rican samples were collected in January (dry season) and June (wet season) of 2002, and the same trees were sampled during each field campaign. Foliage at Cauaxí and Tapajós was collected in July 2001 and June 1999, respectively. Leaves were removed from full sunlight positions in the upper canopy, and subsampled for fully expanded leaves only. In nearly all cases, small groups of leaves were collected using a shotgun. When that method failed, we used a large slingshot (Sherril, Charlotte, North Carolina, USA) to shoot a small, heavy canvas bag over a selected branch; this bag was connected to fishing line, which in turn could be used to pull heavy nylon cord over the branch. This cord was then used to break the branch and thereby obtain the leaf samples.

The forests in all sites are highly diverse, but those on the Osa Peninsula are exceptionally so, perhaps among the most diverse on the planet (Janzen 1983, Kappelle et al. 2003), and also characterized by unusually tall canopies. Thus for these sites we selected a few species that were relatively common and likely to display a range of foliar nutrient concentrations, and concentrated on evaluating changes in these species across soil types and seasons. In contrast, two large sampling campaigns aimed at maximizing the diversity of species represented were carried out in Tapajós and Cauaxí.

In all cases, foliar samples were air dried in the field, transported to the laboratory (in the U.S. or the University of Brasilia, Brazil), and oven-dried for 72 h at 60°C. Foliar samples were ground to a fine powder using a Wiley Mill (Thomas Scientific, Swedesboro, New Jersey, USA). Foliar carbon (C) and N were analyzed using a Carlo Erba EA 1110 elemental analyzer (CE Elantech, Lakewood, New Jersey, USA), and foliar P using a sulfuric acid/hydrogen peroxide digest and a colorimetric P analysis on an Alpkem autoanalyzer (OI Analytical, College Station, Texas, USA), using the ammonium molybdate ascorbic acid method (Kuo 1996). Data on every species analyzed across the sites are available in Appendix A.

Literature synthesis

We assembled data on foliar N and P values for mature tropical forests from a range of literature sources (Appendix B). When data from published studies were reported for individual species, those values were entered into a species-specific database (Appendix A; hereafter referred to as SDB) that included the relevant sites from the Reich and Oleskyn (2004) synthesis, the new data reported here, and those from several other tropical sites, most notably Reserva Samuel in the Brazilian Amazon (Martinelli et al. 2000), Korup National Park in Cameroon (Chuyong et al. 2000), the Panama Canal Watershed (Santiago et al. 2005), Maracá Island in northeastern Brazil (Thompson et al. 1992), and Hainan Island in southeastern China (Han et al. 2005). The new combined database represents more than a sixfold increase to the tropical forest portion of the Reich and Oleskyn (2004) data set, and roughly a 50-fold increase in the number of species representing the lowland forests of Latin America.

In addition, as pointed out by Hedin (2004), there is merit in considering large-scale patterns from both a species-specific and overall site mean perspective; species-specific data are not available for a number of tropical sites. Thus we assembled a second database (means database, MDB) containing only mean foliar N and P values (Appendix B); these data were then used to examine large-scale relationships with latitude and MAP. The data include means of all the sites represented in the species-specific data, as well as additional values from McGroddy et al. (2004) and Vitousek and Sanford (1986). We note that the values in this data set vary considerably in how comprehensively a site was sampled; in some cases the mean value is from a very small number of samples and species, while in others it reflects >100 species from a single site (Cauaxí and Reserva Samuel). The current general lack of data from tropical forests means that a more thorough standardized comparison of site means is simply not possible.

Data analysis

When viewed across the entire species-specific database, or for nearly every major individual site, the data for foliar N and P exhibited significant heteroscedascity and nonnormal distributions. Thus analyses for significant differences among sites, families, and/or soil type were performed on base-10 log-transformed data; such transformations eliminated any major departures from normality or homogeneity of variances and are common in analyses of leaf traits (e.g., Reich et al. 1999, Wright et al. 2004). Statistical analyses were performed using the SPSS v. 11.0 software package (SPSS, Chicago, Illinois, USA) or the (S)MATR standardized major axis software (D. Warton, *unpublished software*).

Linear regression was used to analyze relationships between foliar N:P ratios and both latitude and mean annual precipitation. Standardized major axis estimation (SMA) assumes error in both X and Y dimensions and does not require an arbitrary independent predictor, and thus was used to assess the relationships between foliar N and P and their differences among major soil classes. Analyses of the Costa Rican data were done via two-way ANOVAs; in the case of seasonal differences in foliar N and P, a repeated-measures ANOVA was used because the same trees were measured in each season. ANOVA was also used to examine differences in mean leaf traits across soil types and well-represented families

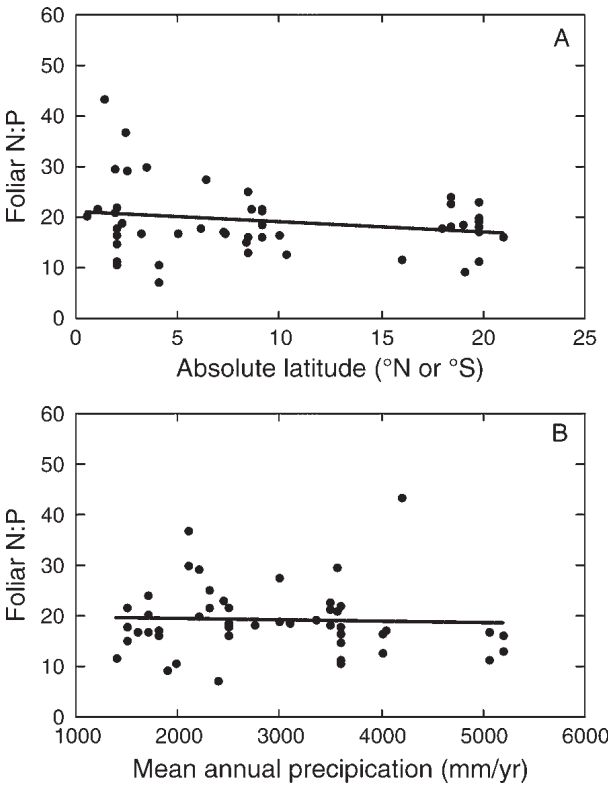

FIG. 1. Mean foliar N:P values (mass basis) for 47 evergreen tropical forest sites (Appendix B) vs. (A) the absolute value of latitude and (B) mean annual precipitation. No significant relationship exists for either latitude or precipitation.

in the SDB. Analyses of normality and homogeneity of variance for all ANOVAs and regressions were done with a Shapiro-Wilk W test and Levine's test, respectively. In all ANOVAs, where significant differences were found, further analyses of differences were evaluated using a post hoc Tukey's hsd test.

RESULTS

Environmental controls over foliar N:P ratios

We present all N:P ratios on a mass (rather than a molar) basis. The overall mean (±SD) of foliar N:P values in the means database (MDB; Appendix B) was 19.5 ± 6.7, and individual site means ranged from a low of 7.5 in a montane Columbian site (Vera et al. 1999) to a high of 43.5 in lowland forest in Sarawak, Malaysia (Peace and Macdonald 1981). However, the latitudinal patterns that emerge at a global scale do not occur within the tropics alone. Regression of absolute latitude vs. log-transformed foliar N:P values showed no significant relationship ($r^2 = 0.005$). Because there was no predictive value in latitude, Fig. 1A shows the pattern for nontransformed data for easier interpretation. We also assembled mean annual precipitation values for all 47 sites in the MDB, but at this pantropical scale, no relationship between mean foliar N:P values and rainfall is seen across sites that range from 1500 mm to >5000 mm of annual precipitation (Fig. 1B; for log-transformed data, $r^2 = 0.004$).

In contrast, there are significant differences in foliar N:P values associated with soil P availability and/or soil order. For example, at the site-specific scale, foliar P is significantly higher ($F = 6.2$, df = 1, 4, $P < 0.01$), and foliar N:P significantly lower ($F = 5.6$, df = 1, 4, $P < 0.01$), across all species common to both the Costa Rican Mollisols and the neighboring Ultisols. These differences mirror significant differences in plant-available and total soil P pools between the two soil types; for example, labile P (the sum of resin- and bicarbonate-extractable pools) is 21.3 μg P/g of soil on the Ultisols vs. 41.6 μg P/g of soil on the Mollisols (Cleveland et al. 2002, Townsend et al. 2002). Likewise, while the Costa Rican Ultisols are P poor in a global context, they are relatively P rich for highly weathered tropical soils (Cleveland et al. 2002). For example, total P in the Costa Rican Ultisols is approximately twice that at Tapajós, and plant-available P fractions are also ~25% higher in the Costa Rican sites (Silver et al. 2000, Townsend et al. 2002, Olander et al. 2005). Mean foliar N:P values for the Costa Rican and Brazilian sites reflect these differences. In Costa Rica, the mean N:P value for the Ultisols is 16.4 ± 4.7, a value that is significantly lower ($F = 8.6$, df = 1, 53, $P < 0.01$) than that from Tapajós (29.8 ± 6.1).

At a larger scale, soil order differences in foliar N:P also emerge. Within the MDB, the mean foliar N:P value for sites on Oxisols and Ultisols is 23.5 ± 6.1, vs. 16.7 ± 3.9 for forests on all other soil orders except nutrient-poor sands; the sandy sites had an intermediate value of 20.1 ± 9.8. Within the species-specific database (SDB), the mean foliar N:P value for all species sampled on Oxisols and Ultisols is 26.1 ± 8.9, a value that is significantly higher ($F = 62.3$, df = 1, 564, $P < 0.001$) than the mean of 17.2 ± 4.4 for species from all other soil orders (Fig. 2C). The difference in foliar N:P values with soil class are largely a function of P content; foliar P is significantly lower on Oxisols and Ultisols (Fig. 2B; $F = 42.1$, df = 1, 564, $P < 0.001$), while no equivalent difference is seen for foliar N (Fig. 2A). In addition, the relationship between foliar N and P content is different for Oxisols and Ultisols as compared to all other soil orders (Fig. 3). The Standardized Major Axis for Oxisols and Ultisols has a slope of 0.56, a value that is significantly lower (test statistic = 4.4; $P < 0.05$) than the slope of 0.65 found for all other soils.

Finally, data from our Costa Rican sites showed variation in foliar N:P ratios with seasonal patterns in rainfall. Foliar P concentrations were significantly elevated in the dry season; when averaged across all species, foliar P was ~25% higher in the dry season in both P-poor and P-rich sites (Fig. 4). Foliar N did not vary with season, but the changes in P concentrations resulted in a significant increase ($F = 4.8$, df = 1, 6, $P < 0.01$) in foliar N:P ratios over a five-month period between the dry and mid-wet seasons.

Species controls over foliar N:P ratios

Variation among species is perhaps the most striking feature of the data presented here. Within the SDB, foliar N:P values on Oxisols and Ultisols range from 5.8 to 69.0; across all other soil orders, they vary from a low of 8.1 to a high of 43.8 (Fig. 2C). Trees growing on P-poor Ultisols and Oxisols also display a significantly greater variance (Levine's test; $P < 0.05$) for foliar N:P than do those on more fertile soils, but trees on P-poor soils have a significantly lower variance for foliar P (Levine's test, $P < 0.05$). Thus the larger range in foliar N:P values on the Oxisols and Ultisols is influenced by both foliar N and P contents, as can be seen in Fig. 2. However, while foliar N is a strong control over the range in N:P values, leguminous trees do not have significantly different relationships between N and P, or between soil orders, than those seen for all other species combined.

In order to further explore biotic controls over foliar N:P values, we also analyzed differences among the nine most abundant families found on Oxisols and Ultisols. Analyses of variance showed significant differences among families for foliar N ($F = 13.9$, df = 8, 257, $P < 0.001$), foliar P ($F = 5.1$, df = 8, 257, $P < 0.01$), and foliar N:P ($F = 4.8$, df = 8, 257, $P < 0.01$). The strongest separation among families was seen for foliar N content, with legumes exhibiting the highest values (Fig. 5A) and the Burseraceae and Myristicaceae the lowest. Less separation was seen for foliar P, though the overall patterns were somewhat similar to foliar N, with Fabaceae, Rutaceae, and Euphorbiaceae displaying high values, while the Burseraceae and Myristicaceae were again among the lowest (Fig. 5B). However, the statistical groupings in foliar N:P values across families are not equivalent to those for either nutrient alone and show the least separation among the nine families analyzed (Fig. 5C).

Finally, a qualitative comparison of foliar N:P ratios for tropical vs. temperate trees emphasized the substantially greater variation seen in tropical regions (Fig. 6). For example, the range in foliar N:P values for all 120 temperate tree species in the Reich and Oleskyn (2004) data set is 19.9. This value is exceeded by the range for several individual tropical sites represented in the SDB: Reserva Samuel (63.3), Cauaxí (49.2), Tapajós (33.3), the Hawaiian Islands (32.6), and Puerto Rico (25.1). Similarly, the ranges for nearly all major families in the SDB exceeded that for the entire temperate data set (Fig. 6).

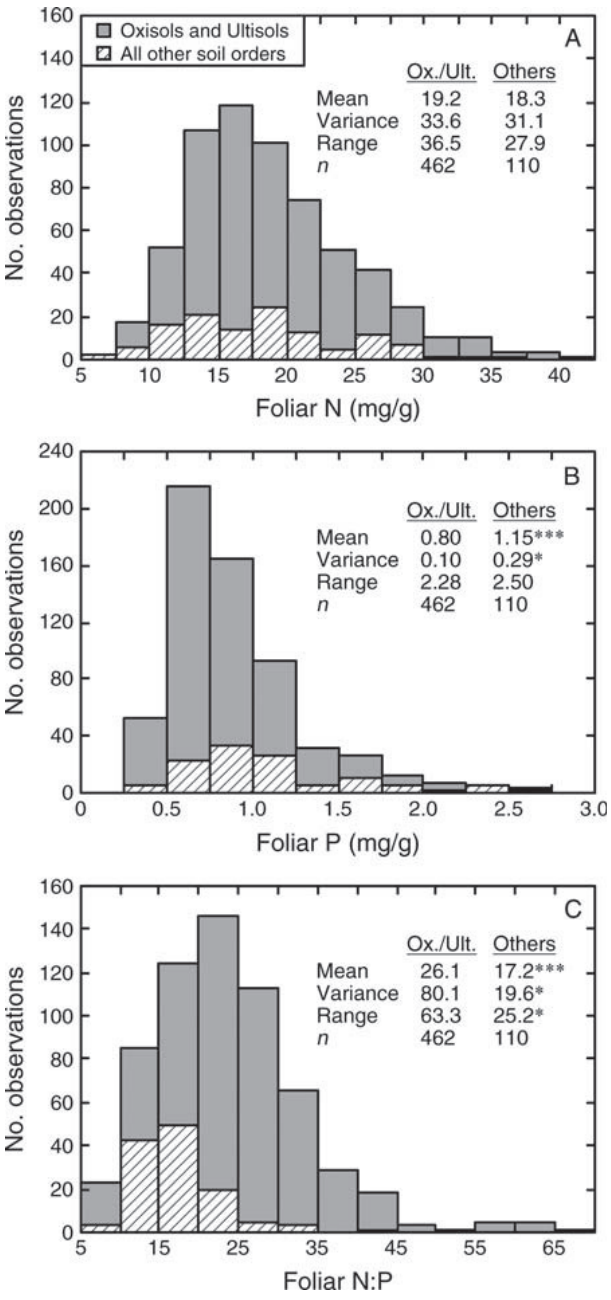

FIG. 2. Histograms of species-specific (A) foliar N, (B) foliar P, and (C) N:P ratios (mass basis) from the species-specific database (Appendix A), separated by two soil classes: P-poor Oxisols and Ultisols (solid bars), and all other soil orders (hatched bars). Asterisks in a given panel denote significant differences between soil classes for a given variable at the $P < 0.001$ (***) or $P < 0.05$ (*) level. See *Results* for details on statistical analyses.

DISCUSSION

The influence of climate

In contrast to the global analyses summarized in Hedin (2004), our data suggest that within the tropical biome, latitudinal gradients in foliar N and P content do not exist (Fig. 1A). This is not necessarily surprising, because as opposed to the global scale, coherent differences in the factors that may cause foliar N:P variation are not likely to occur within tropical latitudes. However, one stated implication of the global latitudinal patterns was that climate exerts a significant influence on N:P stoichiometry (e.g., Reich and Oleskyn 2004). With the exception of upper-elevation montane forests, rainfall is the major source of climate variation both across the tropics and within a given site. At a pantropical scale, both annual rainfall and its seasonal-

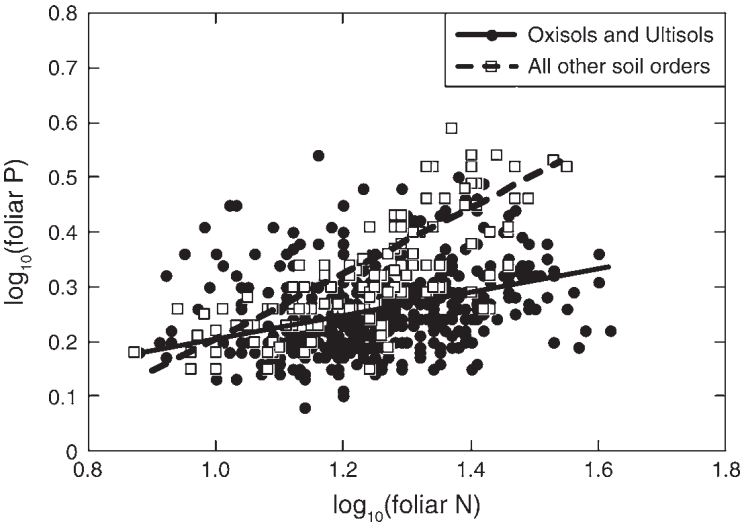

FIG. 3. Foliar N vs. foliar P content for all species in the species-specific database (Appendix A). The foliar concentration values (mg/g) were log-transformed (base 10) prior to analysis and are separated by two soil classes: Oxisols and Ultisols (solid circles), and all other soil orders (open squares). Regression lines are based on Standardized Major Axis estimation (Warton and Weber 2002), which shows a significantly lower slope ($P < 0.05$) for the Oxisols and Ultisols.

ity vary tremendously, and the influence of such variation on basic ecosystem processes (such as net primary production and decomposition) remains uncertain and widely debated (Schuur 2003). Our data show that at this same scale, there is no correspondence between annual rainfall and foliar N:P values (Fig. 1B). This result differs from a trend of declining foliar N:P values with increasing rainfall in Maui (Schuur and Matson 2001) and Panama (Santiago et al. 2005), suggesting that while total rainfall may have an influence on nutrient supply and its link to canopy chemistry, that influence is minor compared to those caused by species differences and soil type.

In contrast, the Costa Rican data displayed surprisingly large variation in foliar P concentrations between dry and wet seasons (Fig. 4), a change that occurred on both P-rich and P-poor soils. The cause for seasonal differences in foliar P is unknown, although the dry-season increase in foliar P is associated with similar increases in both soil microbial and resin-extractable P (Cleveland et al. 2004*b*). Moreover, the foliar increase is clearly a direct result of seasonal dynamics in P cycling (as opposed to an artifact of other aspects of foliar chemistry), as multiple other foliar nutrients, including N and all three major base cations (A. R. Townsend, *unpublished data*), do not change with season.

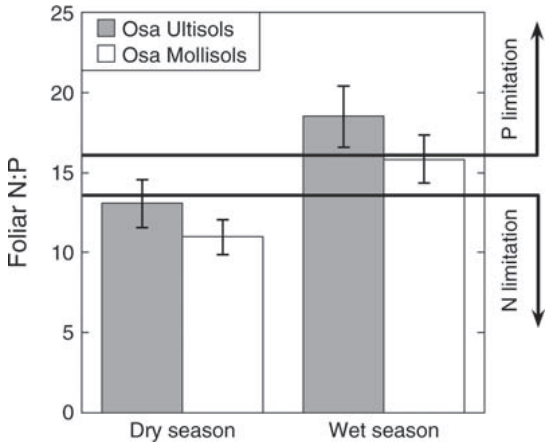

FIG. 4. Foliar N:P ratios (mass basis, averaged across all species sampled; mean ± SE) for dry and wet seasons in forests on Mollisol (MF) and Ultisol (UF) soils in southwest Costa Rica. Lines denoting N vs. P limitation are not derived from known limitations in these sites, but rather from suggested values in several recent studies (e.g., Aerts and Chapin 2000, Tessier and Raynal 2003, Güsewell 2004, Reich and Oleskyn 2004).

It is intriguing to place this seasonal variation in foliar P in the context of attempts to use foliar N:P ratios as an index of N vs. P limitation (e.g., Koerselmann and Mueleman 1996, Aerts and Chapin 2000, Sterner and Elser 2002, Tessier and Raynal 2003, Güsewell 2004, Richardson et al. 2004). Aerts and Chapin (2000) suggest that N limitation likely occurs at N:P ratios <14, with P limitation probable at values >16. These and other authors (e.g., Sterner and Elser 2002, Reich and Oleskyn 2004) are careful to point out that life-form and even species level variation in nutrient requirements are likely to create different breakpoints between N and P limitation, but nonetheless, it is instructive to view our data in light of the hypothesized transition at N:P values of 14–16 (Fig. 4). If one sampled foliage only in the dry season, this stoichiometric perspective would suggest N limitation in all soil types, despite the fact that foliar N does not vary among soil types, whereas foliar P does. Five months later, in the wet season, the P-poor Ultisols displayed an average N:P value of 19, suggesting P limitation, and even the P-rich MF site approached the threshold value of 16 (Fig. 4).

Species vs. the environment

The sizable range and variance in foliar N:P ratios in nearly every site and family we analyzed (Figs. 3 and 6) suggest that local-scale species diversity, rather than environmental factors, may exert the strongest control on variation in foliar nutrients within tropical forests.

Species-level differences in nutrient requirements are no surprise, nor are differences in community structure (e.g., Gentry 1981, 1990, Clark et al. 1999), nutrient use (Silver 1994, Paoli et al. 2005), and foliar nutrient concentration (Fig. 2) with soil type. However, the variability in tropical N:P ratios challenges their use as a larger-scale predictive index. For example, the variance in mean foliar N:P ratios across all 47 sites represented in the means database is 45.5; in comparison, it was 86.6 and 67.9 for Reserva Samuel and Cauaxí species alone, respectively. Data from the RAINFOR consortium of sites across the Amazon Basin suggest a similar conclusion (J. Lloyd, *personal communication*; S. Patina and R. Paiva, *unpublished data*). Even in single, highly P-deficient sites, such as those at Cauaxí, Tapajós, and Reserva Samuel, the large range in foliar N and P contents highlights a diversity of physiological strategies in response to the P-poor environment, and suggests that the extent of limitation by any given nutrient may vary considerably among individual species within a single site. For example, Davidson et al. (2004) showed that both net primary productivity (NPP) and foliar nutrient responses to N and P fertilization in a secondary forest located on P-poor soils in the eastern Amazon were highly variable across species, with some responding to P additions, while others responded most strongly to N.

These variable responses reflect the high diversity of life history and physiological strategies in tropical forests (Gentry 1990), and suggest that N:P ratios may more strongly reflect life history strategies and physiological capacities than environmental factors such as soil type or climate (cf. Ågren 2004, Niklas et al. 2005). For example, species level differences in foliar and litter nutrients in a West African forest were associated with ectomycorrhizal abundance (Chuyong et. al 2000), a characteristic that is common in, but highly variable across, tropical forests (Malloch et al. 1980). Likewise, leguminous trees comprise a significant fraction of many tropical forests (Crews 1999, Vitousek and Field 1999), and might be expected to display at least high foliar N concentrations (McKey 1994) and perhaps significantly different nutrient ratios than families that lack N-fixing symbioses. Indeed, three separate studies of Amazonian forests showed significantly higher foliar N contents in legumes vs. other families analyzed (Thompson et al. 1992, Senna 1996, Martinelli et al. 2000), and we find a similar pattern in the database assembled here (Fig. 5A).

However, the higher N contents in legumes do not lead to consistently different N:P ratios or foliar P contents (Fig. 5B, C), or to a significantly different relationship between foliar N and P concentrations. The variance in N:P ratios of legumes alone is also nearly as high as that for the entire species-specific database (SDB), higher than all other families analyzed, and higher than all but one of the individual tropical sites. Thus legumes as a group do not lead to predictable differences in canopy N:P values. Likewise, while some patterns are suggested by Fig. 5 (e.g., species in the Euphorbiaceae tend to have low N:P values while those in the Sapotaceae are relatively high), none of the major families analyzed have especially notable differences in

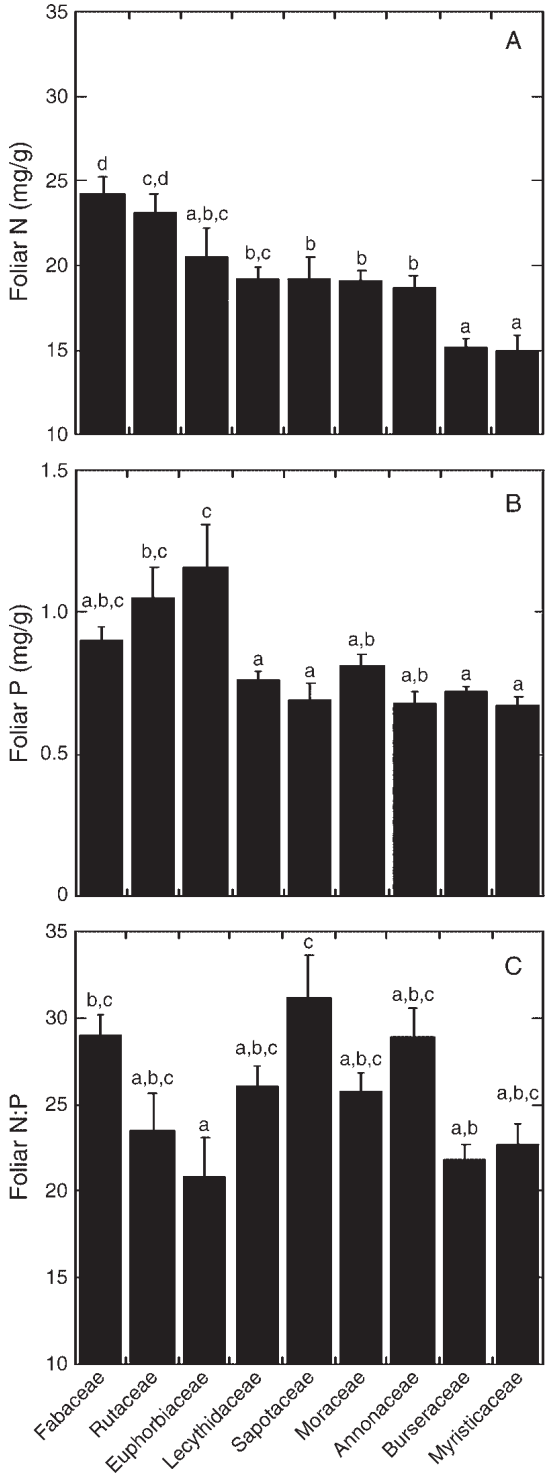

FIG. 5. (A) Foliar N, (B) foliar P, and (C) N:P ratios (mass basis; mean ± SE) for the nine most abundant families on Oxisols and Ultisols. Each family had a minimum of 10 representatives. Letters denote significant differences at the $P < 0.05$ level; see *Results* for details on statistical analyses.

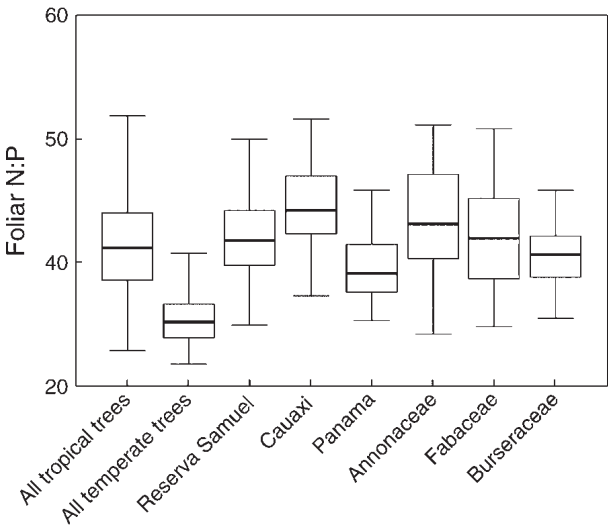

FIG. 6. Box plot of foliar N:P values (mass basis) for all tropical species in Appendix A, comprising 120 temperate tree species across a range of sites as described by Reich and Oleskyn (2004), three of the individual tropical sites included in Appendix A, and three of the most abundant families represented in this database. The three site-specific and family box plots include the most and least variable for each category (minimum of 20 values). Each box denotes the median and interquartile ranges for a given category.

N:P ratios. Again, this fact highlights the significance (and difficulty) of high tree diversity in tropical forests. Even with family level resolution, while a family may share a trait that could create predictable patterns in canopy chemistry (e.g., the ability to form N-fixing symbioses), as a whole they still tend to be enormously diverse groups with variability in other physiological strategies (e.g., mycorrhizal association) that can create large variation in foliar nutrient concentrations, as exemplified by Fig. 6. Moreover, even mean values for a large number of species in a given site will not necessarily reflect the true "whole-community" N:P value, as this will depend on both the relative abundance and size of individuals within each species (Ackerly et al. 2002).

While it may be difficult to predict how high species diversity controls patterns in canopy chemistry and nutrient cycling, local-scale variation in nutrient requirements still has the potential to affect ecosystem processes that are relevant at large scales (Sollins 1998). For example, leaf litter decomposition in our Costa Rican sites is dominated by the transfer of dissolved organic material (DOM) from litter to the underlying soils (Cleveland et al. 2006). Those pulses of DOM, in turn, drive much of the observed variability in CO_2 efflux from the soils (Cleveland and Townsend 2006), and the rate at which such DOM is mineralized to CO_2 is also a function of soil nutrient availability (Cleveland and Townsend 2006, Cleveland et al. 2002). Data from these sites show that the nutrient content of litter-generated DOM varies dramatically among species that co-occur in a single soil type (Cleveland et al. 2004*a*). Thus it is entirely possible that variations in foliar nutrient content translate into differences in the nutrient content of DOM, which in turn is likely to affect soil carbon loss and stabilization.

More generally, data from multiple ecosystems show that variations in tissue nutrient concentrations affect decomposition rates and nutrient supply (Melillo et al. 1989, Cebrian 1999, Gholz et al. 2000). Thus nutrient-rich and nutrient-poor tissues, respectively, can drive feedbacks that tend to maintain those relative states (Vitousek 1982). In tropical forests, it remains largely unknown whether species level differences in tissue N and P contents commonly create "hot and cold spots" for nutrient supply, or whether the high diversity results in such canopy-level gradients being averaged out at the soil level.

Tropical forests and global N:P stoichiometry

More than 70 years ago, Alfred Redfield first described the remarkable constraint that exists in the ratios of carbon, nitrogen, and phosphorus in marine phytoplankton (Redfield 1934). Subsequent work to understand the controls over marine Redfield ratios has had an enormous influence on our understanding of ocean biogeochemistry (Falkowski and Woodhead 1992). More recently, several studies have extended the Redfield perspective to terrestrial ecosystems (cf. Reiners 1986, Sterner and Elser 2002, McGroddy et al. 2004), and have argued that while such systems are inherently more variable than the oceans, broadly similar constraints exist. For example, McGroddy et al. (2004) concluded that "the convergence within a factor of two in photosynthetic N:P ratios supports the notion that autotrophic N and P investments are subject to similar physiological constraints across terrestrial and marine ecosystems." At a global scale, there is clearly some support for this statement.

However, prior analyses have been hampered by a scarcity of tropical data, yet tropical forests may contain as much as 50% of the world's aboveground biomass and account for roughly one-third of global NPP (Field et al. 1998). Thus tropical forests exert a strong influence over the stoichiometry of the terrestrial biosphere as a whole. Our database provided the opportunity to consider the contribution of tropical foliage in a new light. For the species-specific data as a whole, molar N:P ratios averaged 53.1 $\pm$ 20.0, more than three times the Redfield N:P ratio of 16, a pattern also noted by McGroddy et al (2004). In addition, the N:P stoichiometry of tropical foliage exhibited perhaps the greatest variability of any major group of photosynthetic organisms. Expressed on a molar basis, N:P ratios across the individual species analyzed here varied by more than an order of magnitude (12.7–152.8), and on either a mass or molar basis exhibited a much broader distribution of N:P ratios than did temperate trees (Fig. 6). Likewise, molar N:P ratios for the site mean

database (Appendix B) averaged 43.2 ± 14.8, and ranged from a low of 16.6 to a high of 96.3. Thus we contend that foliar N:P stoichiometry in tropical forests is in fact not as well constrained as in many other systems, but rather is substantially malleable in response to both environmental and species level controls.

Dealing with diversity

The imprint of soil type on foliar N:P ratios (e.g., Figs. 2–4) shows that despite substantial species variability, the chemistry of the tropical canopy may still provide a useful index of regional variation in nutrient cycling. However, the large variation in N:P values shown in Fig. 6, and the seasonal variation observed in Costa Rica (Fig. 4) and Cameroon (Chuyong et al. 2000), suggest that one-time surveys of just a small percentage of the tree species in a given site will not be reliable indicators of the canopy as a whole. Rather, comprehensive sampling that integrates across time and space is likely required. The logistical challenges of such sampling mean that remotely sensed estimates and indicators of canopy N and P content may be best suited to meeting this goal (Wessman et al. 1988, Martin et al. 1997, Ollinger et al. 2002). Currently, remotely sensed, high spatial and temporal resolution estimates of canopy N content in tropical forests remain an achievable task (Asner and Vitousek 2005), while similar estimates of canopy P still pose a substantial challenge, since P is not directly expressed in optical reflectance data collected by field or satellite systems (Asner et al. 2006).

Instead, P concentrations of upper-canopy foliage are often correlated with specific leaf area (SLA) or thickness, as well as pigment concentrations (Porder et al. 2005). New measurements of leaf water content, which are often close correlates with SLA (Ceccato et al. 2001), may provide an avenue to estimate P concentration remotely. Moreover, recent advances in remote pigment analysis of chlorophyll and carotenoid concentrations from field and spaceborne levels may provide a window into understanding local and regional gradients of P availability (Gitelson et al. 2002, Asner et al. 2005*a*). At this point, the technical limitations outweigh many of these scientific challenges. Very high performance imaging spectrometers are needed to advance the science of canopy chemical analysis from airborne or space-based vantage points, but very few truly "high fidelity" systems are available at this time (Asner et al. 2005*b*).

Conclusions

If the remote-sensing challenges can be met, then regional pictures of canopy N and P content that also contain information about local-scale influences will be available. However, the degree to which such information provides a window into an ecosystem process that cannot be observed from above will depend on a better understanding of what foliar nutrients in the tropics do and do not reflect. The substantial species level variation clearly shows the importance of life history traits and physiological limitations in shaping N:P values (Ågren 2004, Niklas et al. 2005), and such organismal controls will challenge the use of N:P as a broadscale index in highly diverse ecosystems. In addition, unknowns arise from more general uncertainties about the nature of nutrient limitation in tropical forests. Certainly the broad generalizations that often characterize such forests as N-rich, P-poor environments have merit, but they still rely upon a relatively small amount of data and may mask critical variation in the extent and nature of nutrient limitation at multiple scales. For example, the data from Tapajós, Cauaxí, and Reserva Samuel, as well as the fertilization study by Davidson et al. (2004), suggest that even in very P-poor sites, both N and P limitation of individual species may occur. Moreover, the highly weathered nature of many tropical soils means that likely candidates for nutrient limitation are not restricted to N and P alone; calcium (Ca), potassium (K), and/or magnesium (Mg) limitation is also possible and has been demonstrated in at least one lowland forest (Cuevas and Medina 1988). In sites where base cation limitation predominates, foliar N:P ratios will not provide an index of nutrient limitation and may also show even greater cross-species variability.

These uncertainties highlight both the complexity and challenges of understanding tropical forests in a changing world. Taken as a whole, they can be a dominant influence on earth's carbon cycle and climate system (Shukla et al. 1990, Townsend et al. 1992, Malhi et al. 2002, Clark 2004), they house its largest reservoirs of biological diversity (Wilson 1988), and they encompass many regions of explosive sociopolitical change (Myers et al. 2000). Yet despite their global importance, tropical forests remain woefully understudied, especially when one considers their tremendous environmental diversity (Ometto et al. 2005). A more complete understanding of tropical forest ecology across multiple scales, one in which broad generalizations can be rooted in sufficient data, presents one of the grand challenges for ecologists in the coming century.

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APPENDIX A

Foliar nitrogen (N), phosphorus (P), and N:P ratios from individual species in a range of tropical forest sites (*Ecological Archives* E088-008-A1).

APPENDIX B

Mean foliar N:P values, latitude, and mean annual rainfall for 45 evergreen tropical trees (*Ecological Archives* E088-008-A2).